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Studies in *Basidiodendron eyrei* and similar-looking taxa (Auriculariales, Basidiomycota)

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Abstract

Up to the present moment, *Basidiodendron luteogriseum*, the generic type of *Basidiodendron* (Auriculariales, Basidiomycota), was treated as a synonym of *B. eyrei*. Our data show they are not conspecific. The identity of other members of the *B. eyrei* complex, i.e. *B. deminutum* and *B. grandinioides*, is clarified based on morphological and DNA data, and ten new species are described from Eurasia, as well as from North and South America.

Key words: heterobasidiomycetes, phylogeny, taxonomy

Introduction

Basidiodendron Rick is a genus of the *Auriculariales* (Agaricomycetes, Basidiomycota) encompassing 20 accepted species (www.mycobank.org). First introduced by Rick (1938) as monotypic, the genus was re-established by Luck-Allen (1963) for effused wood-inhabiting fungi with gloeocystidia and four-celled, longitudinally septate basidia. The most striking feature of *Basidiodendron*, however, is a peculiar arrangement of basidia: turgid basidial cells are located at the apices of long, sinuous hyphae covered by shields of collapsed basidia along their whole length. This trait is unique among the *Auriculariales*, and it allows morphological differentiation of the genus from other genera of the *Auriculariales* with gloeocystidia, such as *Bourdotia*, *Ductifera*, *Exidiopsis* s.l. etc. (Luck-Allen 1963; Wells and Raitviir 1975; Wojewoda 1982). The phylogenetic study of the *Auriculariales* conducted by Weiss and Oberwinkler (2001) showed five *Basiodiodendron* species in a single cluster, although without statistical support. Kirschner et al. (2010) described a new genus *Ovipoculum* for an anamorphic fungus *O. album* which clustered with two *Basidiodendron* species; however, the question about monophyly of the latter genus was not addressed. Therefore, it is still uncertain if *Basidiodendron* as defined in morphology-based taxonomic works is monophyletic.

The type species of *Basidiodendron*, *B. luteogriseum* Rick, originally described from Brazil, was placed among the synonyms of the European species *B. eyrei* (Wakef.) Luck-Allen (Wells 1959), and this viewpoint has not been questioned. However, the identity of the latter species was interpreted in different ways (Rogers 1935; Pilát 1957; Wells 1959; Luck-Allen 1963; Lowy 1971; Wells and Raitviir 1975; Wojewoda 1982; Kotiranta and Saarenoksa 2005). In particular, the taxonomic status of *Basidiodendron deminutum* (Bourdot) Luck-Allen, *B. rimulentum* (Bourdot & Galzin) Luck-Allen, *B. grandinioides* (Bourdot & Galzin) Luck-Allen and *Bourdotia mucosa* Bourdot & Galzin versus *B. eyrei* has not been satisfactorily clarified. No attempts to revise the taxonomy of *B. eyrei* s.l. with DNA methods have been performed so far. This paper presents a revision of this complex based on available type material and newly collected

specimens from Europe, North and South America, and East Asia. In total, fourteen species are dealt with, and ten of them are introduced as new to science.

Material and methods

Morphological study. Type specimens and other collections from herbaria H, O, S, LE, PC, FH, TU, S, MG and URM were studied. Herbarium acronyms are given according to Thiers (2020). All measurements were made from microscopic slides mounted in Cotton Blue, using phase contrast and oil immersion lens (Leitz Diaplan microscope, ×1250 magnification). At least 10–20 gloeocystidia and turgid basidia, and 20–30 basidiospores were measured per each specimen studied. The following abbreviations are used in morphological descriptions: L – mean basidiospore length, W – mean basidiospore width, Q' – length / width ratio, Q – mean length / width ratio, n – number of measurements per specimens measured.

Measuring basidiospores in the *B. eyrei* complex often finds difficulty in a variable spore shape, and, consequently, in defining of what should be considered a spore length and a spore width. Identification of the basidiospore shape "normal" to a given species / specimen starts from the study of the apiculus arrangement (phase contrast illumination and Cotton Blue as a mountant are compulsory). In some species (*B. deminutum*, *B. grandinioides* etc.), most basidiospores are ellipsoid and they possess a conventionally arranged ("regular") apiculus: it is located approximately at the top of the spore longest axis which is therefore regarded as the basidiospore length while the transversal axis represents the basidiospore width. However, some basidiospores in the same specimen may have an apiculus shifted to their ventral side ("eccentric" apiculus). In this case, the longest distance between two opposite points of the basidiospore contour is counted as a spore length, the apiculus placement notwithstanding. In turn, *Basidiodendron eyrei*, *B. luteogriseum* and other species with nearly globose basidiospores represent a different case: in most spores, the apiculus is located at the top of a shorter axis dividing a basidiospore into two almost symmetrical halves ("compressed-subglobose" basidiospores). Here this axis is

considered a basidiospore length for all cases, including a minority of basidiospores with an eccentric apiculus.

DNA study. In total, 31 specimens were selected for DNA study (Table 1). We performed PCR directly from small fragments of dried basidiocarps without prior DNA purification using Phire Plant Direct PCR Kit (Thermo Scientific, USA) according to the manufacturer's instructions. The following primers were used for both amplification and sequencing: the primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990) for the nrITS1-5.8S-ITS2 region, primers EF1-983F and EF1-1567R (Rehner and Buckley 2005) for a part of the *tef1* region, primers JS1 (Landvik 1996) and LR5 (Vilgalys and Hester 1990) for D1-D3 domains of nrLSU region. PCR products were purified applying the GeneJET Gel Extraction and DNA Cleanup Micro Kit (Thermo Scientific, USA). Sequencing was performed with an ABI model 3500 Genetic Analyzer (Applied Biosystems, USA). Raw data were edited and assembled in MEGA 7 (Kumar et al. 2016). Molecular studies were mostly carried out at the Center for collective use of scientific equipment "Cellular and molecular technology of studying plants and fungi" (Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg, Russia).

Phylogenetic analyses. For this study, 27 nrITS, 18 *tef1* and 12 nrLSU sequences were generated (Table 1). Additionally, 58 nrITS and 57 nrLSU sequences, including the outgroup, were retrieved from GenBank and UNITE (www.ncbi.nlm.nih.gov/genbank/; https://unite.ut.ee/). Sequences were aligned with the MAFFT version 7 web tool (http://mafft.cbrc.jp/alignment/server/). The strategy G-INS-i was selected for nrLSU and *tef1* datasets, and the Q-INS-i option for nrITS dataset. A partition homogeneity test (PHT) between nrITS and *tef1* datasets was performed with PAUP 4.0b10* (Swofford 2002). The PHT resulted in a *p* value of 0.065, indicating that no significant incongruence was detected between nrITS and *tef1* datasets. Phylogenetic reconstructions were performed with Maximum likelihood (ML) and Bayesian (BA) analyses. Before the analyses, the best-fit substitution model for the alignment was estimated based on the Akaike Information Criterion (AIC) using FindModel web

server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). HKY model was chosen for nrITS dataset and GTR model was chosen for nrITS+*tef1* and nrITS+nrLSU datasets. Maximum likelihood analysis was run on RAxML servers, v.0.9.0 (Kozlov et al. 2019) with one hundred rapid bootstrap replicates. Bayesian analyses was performed with MrBayes 3.2.5 software (Ronquist et al. 2012), for two independent runs, each with 5 million generations (for nrITS dataset), 4 million generations (for nrITS+nrLSU dataset) and 7 million generations (for nrITS+*tef1* dataset), under described models and four chains with sampling every 100 generations. To check for convergence of MCMC analyses and to get estimates of the posterior distribution of parameter values Tracer v1.6 was used (Rambaut et al. 2014). We accepted the result where the ESS (Effective Sample Size) was above 200 and the PSRF (Potential Scale Reduction Factor) was close to 1. Pairwise distances between ITS and *tef1* sequences were calculated using p-distance methods and Maximum Composite Likelihood model in MEGA 7 program.

Newly generated sequences have been deposited in GenBank with accession numbers given in Table 1. Sequenced specimens treated below are marked by an asterisk.

Results

Here we define the *B. eyrei* complex based on comparatively short basidia (in most cases less than 12 µm long) and small (not exceeding 6 µm in a largest dimension) ellipsoid, compressed-subglobose or globose basidiospores. In a few extra-European species treated below, basidiospores may reach 8 µm in length but then they usually possess an asymmetric, eccentric apiculus. *Basidiodendron caesiocinereum* (Höhn. & Litsch.) Luck-Allen s.l. has on average longer basidia (12–22 µm long) and larger, globose or compressed-subglobose basidiospores (5–9 µm in diam.) bearing a very distinct, regular apiculus 1–2 µm long. Moreover, basidiospores in some specimens of *B. caesiocinereum* are ornamented by small warts easily visible in Cotton Blue while they are smooth in *B. eyrei* and sibling species.

Three datasets were prepared for the present study: (1) nrITS + nrLSU dataset used to reconstruct a general topology of the *Auriculariales*, with special emphasis on *Basidiodendron* spp., (2) nrITS and (3) nrITS + *tef1* datasets were limited to the *Basidiodendron eyrei* complex.

(1) The final alignment contained 1650 characters (including gaps). The overall topologies of the ML and BI trees were nearly identical (Fig. 1). They placed all *Basidiodendron* species involved in the analyses (including a newly sequenced specimen of *B. luteogriseum*, the generic type) in one strongly supported clade (bs =100, pp =1). This clade was recovered as a sister lineage of the *Bourdotia – Ductifera* clade, in correspondence with the earlier study by Weiss & Oberwinkler (2001). However, our dataset was limited to the *Basidiodendron* species with small- or medium-sized, asymmetric or globose spores (i.e. to the *B. eyrei* and *B. caesiocinereum* complexes) and two highly deviating nrLSU sequences of *B. cinereum* and *B. rimosum* available in GenBank were excluded from the analyses. Therefore, the question about monophyly of the genus as defined by Luck-Allen (1963) has been left for a future study.

(2) The final alignment contained 622 characters (including gaps). The overall topologies of the ML and BI trees were nearly identical (Supplement) and split representatives of the *B. eyrei* into six strongly supported clades. Nine ITS sequences obtained from European, Asian and North American specimens morphologically identical to the type material of *B. eyrei* and possessing characteristic compressed-subglobose basidiospores clustered with two ITS sequences of East Asian collections (*Kotiranta 26050* and *Spirin 19013*) having globose basidiospores with higher Q values and longer gloeocystidia. ITS sequences of both latter specimens differ from *B. eyrei* sensu typi in nine base pairs (1% difference). Since this genetic distance is seemingly congruous to the morphological differences, we consider it as minimal species-specific difference in the *B. eyrei* complex and introduce a new species, *B. alni*, based on the two aforementioned specimens. ITS sequences of four other species described or reintroduced in this study, namely *B. eyrei* s. typi, *B. globisporum*, *B. grandinioides*, and *B. salebrosum*, show smaller infraspecific variation (1–4 bp difference) than in the case of *B. alni – B. eyrei*, and we could not connect it with

geographic, ecological or morphological traits. However, three morphologically highly similar specimens, all found on dry coniferous wood in subalpine forests of Russian Far East and Canada (Alberta) and tentatively labelled as *B. olivaceum*, revealed ITS sequence differences comparable with those in *B. alni – B. eyrei* clade (8–11 bp). This contradiction between morphological and ecological data on one side and ITS-based phylogeny on another prompted us to produce and analyse an ITS + *tef1* dataset.

(3) The final alignment contained 1185 characters (including gaps). The overall topologies of the ML and BI trees were nearly identical. They split the *B. eyrei* complex into fourteen groups, in good accordance with morphological and ecological data, which we interpret as separate species. Sequences of *B. olivaceum* cluster together with a high support (Fig. 2).

In general, *Basidiodendron* spp. produce rather insignificant basidiocarps and thus they are rarely collected by researchers. This was our reason to describe four species, *B. caucasicum*, *B. iniquum*, *B. microsporum*, and *B. remotum*, based on the type specimens only.

The actual diversity in the *B. eyrei* complex seems to be higher than presented below. In particular, sequences of *B. eyrei* and *B. grandinioides* published by Weiss and Oberwinkler (2001) and Sotome et al. (2014) have no close matches in our dataset. Geographic, ecological and morphological traits of fourteen species treated below are briefly summarized in Table 2.

Taxonomy

Basidiodendron alni Spirin & V. Malysheva, sp. nov. – Fig. 3

MB 834768

Holotype. Russia. Krasnoyarsk Reg.: Evenk Autonomous Dist., Podkamennaya Tunguska, *Alnus hirsuta*, 8.VIII.2013 *Kotiranta 26050** (H 7024641, isotype – LE).

Etymology: alni (Lat.) – from *Alnus*, the host tree genus

Basidiocarps effused, covering a few cm, first pruinose, smooth, arid, pale cream-coloured to greyish, then continuous, smooth, waxy or partly gelatinized, cream-coloured to pale ochraceous,

0.03–0.05 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, thin- or slightly thick-walled, subicular hyphae subparallel, 2–3 µm in diam., subhymenial hyphae more or less clearly ascending, 1.5–2 (–2.5) µm in diam. Gloeocystidia abundant, tapering (subfusiform to bottle-shaped), normally in groups of 3–6, (26–) 29–66 (–68) × (3.2–) 3.3–6.0 (–6.1) µm (n = 30/2); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 35 × 2–3 µm; basidia four-celled, (8.9–) 9.1–11.3 (–11.6) × (5.8–) 6.0–7.8 (–8.0) µm (n = 24/2), senescent basidia slightly thick-walled, sterigmata up to 6 × 1.5 µm. Basidiospores thin-walled or with indistinctly thickened wall, globose to compressed-subglobose, (4.0–) 4.1–5.0 (–5.1) × (4.0–) 4.2–5.0 µm (n = 60/2), L = 4.40–4.65, W = 4.45–4.72, Q' = 0.9–1.0 (–1.1), Q = 0.99, apiculus rather small, regular or slightly eccentric.

Specimens examined. Russia. Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Alnus hirsuta*, 3.IX.2016 *Spirin 10913** (H). Krasnoyarsk Reg. (holotype, see above).

Remarks. *Basidiodendron alni* is introduced here based on two specimens from the Asian part of Russia, both collected from *Alnus hirsuta*. It is most similar to the closely related *B. eyrei* and differs from the latter species in having more regularly globose basidiospores, smaller basidia and longer gloeocystidia. ITS sequences of *B. alni* show 9 bp difference (1%) versus *B. eyrei* while the single available *tef1* sequence of *B. alni* differs from those of *B. eyrei* by 3 bp (0.7%).

Basidiodendron caucasicum Spirin, V. Malysheva & Kotiranta, sp. nov. – Fig. 3

MB 834770

Holotype. Russia. Adygea: Maykop Dist., Guzeripl, *Pinus sylvestris*, 16.IX.2003 *Kotiranta 22569** (H 7045100, isotype – LE).

Etymology: caucasicus (Lat., adj.) – from Caucasus, the geographic area where the species was collected.

Basidiocarps effused, covering a few cm, first reticulate, smooth, pale cream-coloured to greyish, then continuous, more or less regularly tuberculate (grandinioid), waxy or partly gelatinized,

0.05–0.1 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, slightly thick-walled, subicular hyphae subparallel, subhymenial hyphae ascending, 1.5–2 (–2.5) μm in diam. Gloeocystidia abundant, tapering (subfusiform to bottle-shaped), (14.5–) 18–30.5 (–33) × (4.3–) 4.4–5.2 (–5.4) μm (n = 10/1); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 30 × 2 μm; basidia four-celled, (7.2–) 7.3–9.4 (–9.8) × (5.6–) 5.8–7.0 (–7.2) μm (n = 20/1), senescent basidia slightly thick-walled, sterigmata up to 5 × 1.5–2 μm. Basidiospores thin-walled, subglobose or globose, more rarely broadly ellipsoid, (3.9–) 4.0–5.1 (–5.2) × (3.2–) 3.4–4.5 μm (n = 30/1), L = 4.46, W = 3.91, Q' = (1.0–) 1.1–1.3 (–1.4), Q = 1.15, apiculus small, regular.

Remarks. Among the members of *B. eyrei* complex distributed in Europe, only *B. caucasicum* and *B. grandinioides* produce basidiocarps with a regularly tuberculate (grandinioid) hymenophore. Basidiospores of *B. caucasicum* are shorter than in *B. grandinioides*, and they are usually subglobose or globose, versus predominantly ellipsoid basidiospores in *B. grandinioides*. Moreover, the latter species is seemingly restricted to angiosperms while the single specimen of *B. caucasicum* was collected from pine. Two other conifer-dwelling species, *B. deminutum* and *B. globisporum*, differ from *B. caucasicum* by completely smooth basidiocarps and differently shaped basidiospores (Fig. 3). Phylogenetically, *B. caucasicum* is most closely related to *B. olivaceum* distributed in East Asia and North America. However, genetic differences between these species are substantial, i.e. 2.1–3.4% in ITS and 15.8% in *tef1* sequences.

Basidiodendron deminutum (Bourdot) Luck-Allen, Can. J. Bot. 41: 1041, 1963. – Fig. 3

≡ *Sebacina deminuta* Bourdot, C. R. Assoc. Fr. Avancem. Sci. 45: 575, 1922. Lectotype, selected here. France. Aveyron: Causse Noir, *Pinus* sp., 30.XI.1913 *Galzin 14621* (herb. Bourdot 14923) (PC 0706687, studied) (MBT 391136).

= *Bourdotia rimulenta* Bourdot & Galzin, Hymen. France: 51, 1927. Lectotype, selected here. France. Aveyron: Causse Noir, *Pinus* sp., 3.XI.1911 *Galzin 10159* (herb. Bourdot 20192) (PC 0084202, studied) (MBT 391137).

Basidiocarps effused, covering a few cm, first pruinose-reticulate, smooth, arid, pale cream-coloured to greyish, then continuous, smooth or irregularly tuberculate, waxy or partly gelatinized, pale ochraceous to brownish, 0.02–0.05 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, slightly or distinctly thick-walled, subicular hyphae subparallel or interwoven, 2–2.5 (–3) µm in diam., subhymenial hyphae more or less clearly ascending, 1.5–2 (–2.5) µm in diam. Gloeocystidia abundant, tapering (subfusiform to bottle-shaped), (14.5–) 15–40 (–41) × (3.8–) 4.0–7.2 (–7.5) µm (n = 38/5), solitary or rarely in groups of 2–3; hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 20 × 2–3 µm; basidia four-celled, (7.2–) 7.3–9.7 (–10.0) × (5.3–) 5.6–7.2 (–7.3) µm (n = 50/5), senescent basidia slightly thick-walled, sterigmata up to 4 × 1.5–2 µm. Basidiospores thin-walled or with indistinctly thickened wall, cylindrical to broadly ellipsoid, more rarely subglobose or cordate, (3.8–) 4.1–5.6 (–5.8) × (2.8–) 2.9–4.7 (–4.9) µm (n = 150/5), L = 4.60–4.84, W = 3.16–3.91, Q' = (1.1–) 1.2–1.7 (–1.8), Q = 1.23–1.51, apiculus small, regular or occasionally eccentric.

Specimens examined. France. Aveyron: Causse Noir, *Pinus* sp., 25.IV.1910 *Galzin 5686* (herb. Bourdot 9077) (PC 0706685), 13.XI.1913 *Galzin 14618* (herb. Bourdot 13720) (PC 0706684), 30.XI.1913 *Galzin 14621* (herb. Bourdot 14923) (lectotype of *Sebacina deminuta*, see above), 3.XI.1911 *Galzin 10159* (herb. Bourdot 20192) (lectotype of *Bourdotia rimulenta*, see above). Slovenia. Tolmin: Vršič, *Pinus mugo*, 5.VI.2019 *Spirin 12589** (H).

Remarks. *Basidiodendron deminutum* was described from the southern part of France based on several collections of which one is formally designated here as a lectotype. Basidiospores of *B. deminutum* are mostly ellipsoid or cylindrical, with a conventionally arranged apiculus, although spores with an eccentric apiculus are as a rule present in the same collections. In a few specimens, spores of this kind dominate over "normal" ones but we consider this as an

infraspecific variation. So far, *B. deminutum* was detected only on wood of *Pinus* spp. in the southern part of Europe (France and Slovenia).

The taxonomic status of *Bourdotia grandinioides* Bourdot & Galzin, *B. mucosa* Bourdot & Galzin and *B. rimulenta* Bourdot & Galzin was interpreted in literature in two different ways. Most authors (Pilát 1957; Wells 1959; Luck-Allen 1963 etc.) treated them as separate species. In contrast, Ginns (1982: 54) considered *B. grandinioides* as a variety of *Bourdotia deminuta* (Bourdot) Bourdot & Galzin (= *Basidiodendron deminutum*). Bourdot and Galzin (1928) made use of the hierarchical categories subspecies, variety and form and indicated these by different font style and size. In addition, subspecies names were written as full binomials (genus name abridged to the first letter) while for varieties and forms only an epithet was given, immediately following the full taxon name to which they were subordinated. In a few cases Bourdot and Galzin (1928) deviated from this pattern and the names we are dealing with here is one such case. At the end of the treatment of *Bourdotia* a new heading "Formes insuffisamment connues:" is introduced. Under this heading the names *B. rimulenta, B. grandinioides*, and *B. mucosa* are described. There is no explicit indication that these taxa were subordinated to *B. deminuta*, which is the last name before the heading. Unfortunately, the names of these insufficiently known taxa were printed with the "variety" font. This gives us two choices. Either to interpret the names as varieties, in which case we are left without a clear instruction to which species they are subordinate. The alternative is to regard the choice of the "variety" font as a printing error and accept the three names as species. We may get an indication of the correct solution by looking at the end of the treatment of *Helicobasidium* (Bourdot and Galzin 1928: 10–11). Here the same "variety" font is used for four species listed under the heading "Espèces à nous inconnues". Here it is even more clear that the authors did not intend to treat these taxa as varieties. Therefore, we consider *B. grandinioides*, *B. mucosa,* and *B. rimulenta* as validly described taxa at the species rank.

Basidiodendron grandinioides is re-described below as a good species, while *B. mucosa* is placed among the synonyms of *B. eyrei*. The interpretation of *B. rimulenta* is more difficult. The species description was based on two collections, one from *Pinus* (*Galzin 10159*) and another one from *Acer* (*Galzin 13279*). While transferring *B. rimulenta* to *Basidiodendron*, Luck-Allen (1963) designated them both as syntypes. We re-checked these specimens and concluded they are not conspecific, the *Acer*-dwelling one belonging to *B. eyrei* (see below) and the *Pinus*-dwelling one representing *B. deminutum*. The latter collection is widely dominated by cordate basidiospores (depicted by Luck-Allen 1963: 1038), and it was seemingly the main source for the original description, as well as Luck-Allen's reintroduction of this species. Nevertheless, basidiospores of the shape and size typical for other collections of *B. deminutum* are present too, and other microscopic characters point to *B. deminutum*. Therefore, we select the specimen *Galzin 10159* as a lectotype of *B. rimulenta* and place the species as a synonym of *B. deminutum*.

Basidiodenron eyrei (Wakef.) Luck-Allen, Can. J. Bot. 41: 1034, 1963. – Figs. 3, 4

≡ *Sebacina eyrei* Wakef., Trans. Br. Mycol. Soc. 5: 126, 1915. Syntype. United Kingdom. England: Hampshire, Alresford, *Fagus sylvatica*, 4.V.1914 *Eyre* (duplicate in herb. Bourdot 18464) (PC 0084215, studied).

= *Corticium involucrum* Burt, Ann. Mo. Bot. Gard. 13: 271, 1926. Holotype. USA. Vermont: Addison Co., Middlebury, on wood, 27.XI.1894 *Burt* (FH 00526055, studied).

= *Bourdotia mucosa* Bourdot & Galzin, Hyménomyc. de France (Sceaux): 51, 1927. Lectotype. France. Aveyron: St. Sernin, *Prunus cerasus*, 9.IV.1910 *Galzin 5428* (herb. Bourdot 7129) (PC 0084203, studied) (selected by Wells 1959).

Basidiocarps effused, covering a few cm, first pruinose, arid, pale cream-coloured to greyish, then continuous, smooth, waxy or arid, cream-coloured to pale ochraceous, 0.04–0.1 mm thick, sometimes irregularly cracking, old basidiocarps partly gelatinized, watery-greyish to brownish, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, subicular hyphae

thin- or slightly thick-walled, subparallel, 1–3 µm in diam., subhymenial hyphae thin-walled, interwoven or ascending, 1.5–2.5 (–3) µm in diam. Gloeocystidia abundant, tapering (subfusiform to bottle-shaped), normally in groups of 3–6, (16–) 17–45 (–46) × (3.2–) 3.3–7.7 (–7.8) µm (n = 50/5); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 35 × 2–2.5 µm; basidia four-celled, (8.2–) 8.3–13.2 (–13.4) × (5.8–) 6.0–8.2 (–8.3) µm (n = 130/7), senescent basidia slightly thick-walled, sterigmata up to 6 × 1.5 µm. Basidiospores thin-walled or with indistinctly thickened wall, compressed-subglobose to almost globose, (3.7–) 3.8–5.2 (–5.4) × (4.0–) 4.2–5.4 (–5.7) µm (n = 330/11), L = 4.15–4.71, W = 4.66–5.14, Q' = 0.8–1.0, Q = 0.88–0.97, apiculus distinct to rather small, regular or eccentric.

Specimens examined. Canada. British Columbia: Fraser – Fort George Reg. Dist., Mt. Robson Provincial Park, *Picea* sp., 25.VII.2015 *Spirin 8881** (ALTA, H). Estonia. Viljandimaa: Pääsma, *Alnus incana*, 18.IX.2018 *Spirin 12363** (H, TU). Finland. Uusimaa: Helsinki, Viikki, *Salix caprea*, 17.VI.2008 *Miettinen 12700* (H 6012551); Vantaa, Mustavuori, *Sorbus aucuparia*, 11.V.2012 *Miettinen 15359* (H 6012941). France. Aveyron, *Buxus sempervirens*, 13.V.1913 *Galzin 13342* (herb. Bourdot 13970) (PC 0706686), St. Sernin, *Prunus cerasus*, 9.IV.1910 *Galzin 5428* (herb. Bourdot 7129) (lectotype of *Bourdotia mucosa*, see above), Labastide-Pradines, *Acer* sp., 13.V.1913 *Galzin 13279* (herb. Bourdot 20190) (PC 0084219, as *B. rimulenta*). Norway. Aust-Agder: Landvik, Holvannet ved Skiftenes, *Quercus robur*, 22.VIII.1971 *Ryvarden 8205B* (O 104746). Vestfold: Tønsberg, Gullkronene, *Fraxinus excelsior*, 15.IX.2016 *Spirin 11086* (O). Akershus: Asker, Stokkerelva at Åstaddammen, *Alnus incana*, 28.IX.2018 *Spirin 12433, 12435* (O); Bærum, Kjaglidalen, *Ulmus glabra*, 16.IX.2016 *Spirin 11120* (O). Buskerud: Lier, Horn ved Holtsfjorden, *Tilia cordata*, 26.IX.1975 *Ryvarden 13460* (O 104745), Stokkerinden, *Acer platanoides*, 29.IX.2018 *Spirin 12498* (O). Hordaland: Voss, Ringheim, *Corylus avellana*, 18.XI.1951 *Stordal 7310* (O 104747). Russia. Krasnoyarsk Reg.: Evenk Autonomous Dist., Podkamennaya Tunguska, *Betula* sp., 13.VIII.2013 *Kotiranta 26231** (H). Leningrad Reg.: Podporozhie Dist., Vazhinka, *Betula pubescens*, 16.IX.2017 *Spirin*

11386 (H). Nizhny Novgorod Reg.: Arzamas Dist., Pustynsky Nat. Res., *T. cordata*, 12.VIII.2015 *Spirin 9136* (H); Lukoyanov Dist., Panzelka, *T. cordata*, 9.VIII.2016 *Spirin 10579** (H), Razino, *Populus tremula*, 30.VIII.2019 *Spirin 13060* (H), *T. cordata*, 8.VIII.2014 *Spirin 7235* (H), 23.VII.2018 *Spirin 12003** (H), *Quercus robur*, 6.IX.2018 *Spirin 12248* (H); Pavlovo Dist., Chudinovo, *P. tremula*, 15.VII.2016 *Spirin 10260* (H). Spain. Málaga: Estepona, Los Reales de Sierra Bermeja, *Abies pinsapo*, 21.XI.2012 *Miettinen 15918.2** (H). Sweden. Halland: Släp, Särö Västerskog, 6.X.1970 *Eriksson* (O 104741, 104749). Switzerland. Basel-land: Waldenburg, Hölstein, *Fagus sylvatica* (?), 13.VI.2009 *Miettinen 13649** (H). United Kingdom. England: Hampshire, Alresford, *F. sylvatica*, 4.V.1914 *Eyre* (herb. Bourdot 18464) (isosyntype of *Sebacina eyrei*, see above), [probably the same locality], *F. sylvatica*, V.1914 comm. *Bresadola* (herb. Bourdot 13930) (PC). USA. Vermont: Addison Co., Middlebury, on wood, 27.XI.1894 *Burt* (holotype of *Corticium involucrum*, see above). Washington: Jefferson Co., Port Townsend, Fort Worden, *Arbutus menziesii*, 9.X.2014 *Spirin 8313** (H).

Remarks. In almost all cases, *B. eyrei* can be easily identified due to compressed-subglobose basidiospores and angiosperm hosts. It is the most common species of the complex and widely distributed in the temperate zone of Eurasia and North America. However, a few collections studied by us (including the lectotype of *Bourdotia mucosa* and one authentic collection of *B. rimulenta*) possess highly variable, predominantly ellipsoid or cordate basidiospores, (3.2–) 3.8–6.0 (–6.1) × (3.0–) 3.1–5.7 (–5.8) µm (n = 120/4), L = 4.51–5.05, W = 3.81–4.73, Q' = (0.6–) 0.7–1.6 (–1.8), Q = 0.96–1.35 (not included in the species description above). Two of these problematic specimens were sequenced and turned out identical to the rest of *B. eyrei* samples. Rather long basidia and fasciculate gloeocystidia also pointed towards the latter species. We are willing to explain their tricky spore shape and size by unusual sporulation conditions. Specimens of *B. eyrei* dominated by ellipsoid basidiospores can be confused with *B. deminutum* and *B. grandinioides*. In these cases, attention should be paid for basidia and gloeocystidia: basidia are

smaller in the two latter species, and gloeocystidia are solitary or only rarely arranged in pairs or triads.

Basidiodendron globisporum Spirin & V. Malysheva, sp. nov. – Figs. 3, 5

MB 834771

Holotype. Russia. Leningrad Reg.: Kirishi Dist., Shariya, *Picea abies*, 10.VIII.2019 *Spirin 12929** (H, isotype – LE).

Etymology: globisporus (Lat., adj.) – having globose spores.

Basidiocarps effused, covering a few cm, pruinose-reticulate, smooth, waxy, first whitish, then bluish-greyish, in older parts pale ochraceous, 0.02–0.03 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, subicular hyphae thin- or slightly thick-walled and subparallel, 2–3 μm in diam., subhymenial hyphae very thin-walled (quickly collapsing), ascending, 1.5–2 (–2.5) μm in diam. Gloeocystidia abundant, tapering (subfusiform to bottle-shaped), (12–) 15–32 (–33) × (3.0–) 3.2–6.0 (–6.2) μm (n = 42/4), occasionally with a hyphoid apical outgrowth; hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 25 × 2–3 μm; basidia four-celled, (7.8–) 8.8–12.0 (–12.4) × (6.8–) 7.0–9.1 (–9.3) μm (n = 60/4), senescent basidia slightly thick-walled, sterigmata up to 8 × 1.5–2 μm. Basidiospores thin-walled or with indistinctly thickened wall, compressed-subglobose to globose, (4.4–) 4.6–5.8 × (4.6–) 4.8–5.9 (–6.0) μm (n = 150/5), L = 4.95–5.15, W = 5.10–5.33, Q' = 0.9–1.0 (–1.1), Q = 0.96–0.98, apiculus distinct to rather small, regular.

Specimens examined. Russia. Leningrad Reg.: Boksitogorsk Dist., Valgozero, *Picea abies*, 16.VII.2014 *Spirin 7040** (H), Kolp', *P. abies*, 26–28.VII.2016 *Spirin 10326*, 10396* (H); Kirishi Dist. (holotype, see above). Slovenia. Gorenjska: Mojstrana, Triglavska Bistrica, *P. abies*, 28.IX.2019 *Spirin 13450** (H). Sweden. Värmland: Torsby, Fänstjärnskogen, *P. abies*, 9.X.2010 *J. Nordén 7424* (O). USA. New York: Sullivan Co., Wolf Lake, *Tsuga* sp., 15.VIII.2012 *Miettinen 15584** (H).

Remarks. *Basidiodendron globisporum* is morphologically most similar to *B. eyrei*. It differs from the latter species in having slightly larger and more globose basidiospores with a regular apiculus. *Basidiodendron globisporum* is distributed in temperate-boreal coniferous forests where it occurs on rotten wood of *Picea abies* (with one single record on *Tsuga* in USA). On the contrary, *B. eyrei* is almost totally restricted to angiosperm hosts, and it certainly prefers forests dominated by broad-leaved trees.

Basidiodendron grandinioides (Bourdot & Galzin) Luck-Allen, Can. J. Bot. 41: 1039, 1963. – Fig. 3

≡ *Bourdotia grandinioides* Bourdot & Galzin, Hyménomyc. de France (Sceaux): 51, 1927.

Lectotype. France. Aveyron: Betirac, *Populus* sp., 9.VI.1910 *Galzin 5522* (herb. Bourdot 20193) (PC 0084201, studied) (selected by Luck-Allen 1963).

Basidiocarps effused, covering a few cm, first pruinose, smooth, arid, pale cream-coloured to greyish, then continuous, more or less regularly tuberculate (grandinioid), waxy or partly gelatinized, pale ochraceous to brownish, 0.02–0.04 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, thin- or slightly thick-walled, subicular hyphae subparallel, 1.5–2.5 (–3) µm in diam., subhymenial hyphae more or less clearly ascending, 1.5–2 (–2.5) µm in diam. Gloeocystidia abundant, tapering (subfusiform to bottle-shaped), (10–) 12.5–32 (–36) × (3.7–) 3.8–6.6 (–6.8) µm (n = 30/4); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 15 × 2–3 µm; basidia four-celled, (7.8–) 7.9–11.4 (–12.1) × (5.4–) 6.2–8.0 (–8.3) µm (n = 40/4), senescent basidia slightly thick-walled, sterigmata up to 5.5 × 1.5–2 µm. Basidiospores with thin or slightly thickened (0.2–0.3 µm) wall, ellipsoid to broadly ellipsoid, more rarely subglobose, (3.8–) 4.0–6.0 (–6.1) × (3.0–) 3.1–4.9 (–5.0) µm (n = 150/5), L = 4.59–5.13, W = 3.60–4.12, Q' = (1.0–) 1.1–1.5 (–1.6), Q = 1.22–1.36, apiculus small, regular or only in exceptional cases slightly eccentric.

Specimens examined. France. Aveyron: Betirac, *Populus* sp., 9.VI.1910 *Galzin 5522* (herb. Bourdot 20193) (lectotype of *Bourdotia grandinioides*, see above). Norway. Akershus: Asker, Stokkerelva at Åstaddammen, *U. glabra*, 5.V.2016 *Spirin 10031* (O), 28.IX.2018 *Spirin 12437** (O, H). Nord-Tröndelag: Levanger, Östborg, hardwood branch, 16.IX.1972 *Strid 11315** (S F29104). Russia. Khabarovsk Reg.: Solnechnyi Dist., Sonakh, *Quercus mongolica*, 15.VIII.2014 *Spirin 7310* (H).

Remarks. *Basidiodendron grandinioides* is a twin species of *B. deminutum* from which it differs mainly by a grandinioid hymenophore and occurrence on angiosperm hosts. The correct host information is crucial for identification of young basidiocarps with nearly smooth hymenial surface. Another European species with grandinioid hymenophore, *B. caucasicum*, possesses shorter and more globose basidiospores than in *B. grandinioides*. One specimen from Russian Far East (*Spirin 7310*) was tentatively labelled as *B. grandinioides* based on high morphological similarity with collections from Europe and an angiosperm host. Our attempts to sequence it failed. Therefore, the presence of *B. grandinioides* in East Asia should be re-confirmed.

Ginns (1982) placed *B. grandinioides* to the synonyms of *B. fulvum* (Massee) Ginns. The latter species is so far known from two historical collections made in the same locality in New Jersey, USA. We studied one of these specimens (USA. New Jersey: Newfield, rotten *Magnolia*, VIII.1896 *Ellis & Everhart* (Fungi Columbiani #1017, as *Hydnum farinaceum* var. *luxurians*) (H 7052960)) and concluded it cannot be identical with the Eurasian material of *B. grandinioides*. Basidiospores of *B. fulvum* are compressed-subglobose, more similar to *B. eyrei* than to *B. deminutum* but considerably smaller, (2.6–) 2.8–3.6 (–3.7) × 3.2–4.2 µm (n = 30/1), L = 3.18, W = 3.77, Q’ = (0.7–) 0.8–0.9, Q = 0.84. Moreover, basidiocarps of *B. fulvum* are darker, ochraceous-brownish, and basidia are clearly smaller, 6.7–7.8 × 5.2–6.2 µm (n = 10/1) than in *B. grandinioides*.

Basidiodendron iniquum Alvarenga & K.H. Larss., sp. nov. – Fig. 3

MB 834772

Holotype. Brazil. Rondônia: Porto Velho, Parque Natural de Porto Velho, angiosperm wood, 14.III.2012 *Larsson 15469** (O, isotype – H).

Etymology: iniquus (Lat., adj.) – unequal, in reference to variable basidiospores.

Basidiocarps effused, covering a few cm, continuous, smooth, often with irregularly scattered craters, waxy, pale cream-coloured or greyish, 0.04–0.06 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, subicular hyphae scattered, thick-walled, rare, 2.5–3 µm in diam. Gloeocystidia infrequent, arising at different levels from basidia-bearing hyphae, tapering (subfusiform to bottle-shaped), (15–) 18.5–34 (–35) × (4.4–) 4.8–8.2 (–8.8) µm (n = 20/1); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 60 × 1.5–3 µm, hardly discernible due to tightly arranged remnants of collapsed basidia; basidia four-celled, (9.3–) 9.7–13.2 (–13.3) × (7.2–) 7.3–9.1 (–9.2) µm (n = 20/1), senescent basidia slightly thick-walled, sterigmata up to 6 × 1.5–2 µm. Basidiospores thin-walled, ellipsoid to broadly ellipsoid, rarely subglobose, (4.6–) 4.9–6.2 (–6.4) × (4.0–) 4.1–5.2 (–5.3) µm (n = 30/1), L = 5.50, W = 4.63, Q' = (1.0–) 1.1–1.3 (–1.4), Q = 1.19, apiculus distinct, regular or eccentric.

Remarks. Basidiocarps of *B. iniquum* have a very peculiar hyphal arrangement: they consist of a few scattered basal hyphae producing numerous, vertically oriented, densely arranged basidia-bearing hyphae. The same feature occurs also in *B. luteogriseum* which differs from *B. iniquum* mainly in having differently shaped basidiospores. In turn, these "fishbone"-like structures are less prominent in temperate – boreal species treated here. In the latter ones, they occur mostly in senescent basidiocarps. They are often dispersed among richly branched subhymenial hyphae and thus often hardly detectable. *Basidiodendron iniquum* is so far known only from the type locality in the Brazilian Amazon.

Basidiodendron luteogriseum Rick, Brotéria 7: 74, 1938. – Figs. 3, 6

Lectotype, selected here. Brazil. Rio Grande do Sul: Parecy Novo, on wood, 1935 *Rick* (FH 00304775, studied) (MBT 391138).

Basidiocarps effused, covering a few cm, first pruinose, smooth, arid, pale cream-coloured to greyish, then continuous, smooth, cream-coloured to pale ochraceous, 0.05–0.1 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, subicular hyphae scattered, rare, slightly thick-walled, 1.5–2 µm in diam. Gloeocystidia infrequent, usually occurring at the basal parts of basidia-bearing hyphae, tapering (subfusiform to bottle-shaped), (15–) 16–31 (–33) × (3.8–) 3.9–6.6 (–7.0) µm (n = 30/3); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 70 × 2–3 µm; basidia four-celled, (7.3–) 7.8–10.0 (–10.3) × (5.8–) 5.9–8.1 (–8.4) µm (n = 30/2), senescent basidia slightly thick-walled, sterigmata up to 5 × 1.5 µm. Basidiospores thin-walled or with indistinctly thickened wall, compressed-subglobose to globose or rarely broadly ellipsoid, 4.1–5.1 (–5.3) × 4.0–5.1 (–5.4) µm (n = 80/3), L = 4.55–4.75, W = 4.65–4.84, Q' = (0.8–) 0.9–1.1 (–1.2), Q = 0.94–1.03, apiculus distinct to rather small, regular or eccentric.

Specimens examined. Brazil. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Barragem des Moças, angiosperm wood, 20.IV.2013 *Larsson 16022** (O, H). Pará: Caxiuaña, Ferreira Penna Station, angiosperm wood, 15.III.2015 *Larsson 16924* (O, H, MG). Rio Grande do Sul (lectotype, see above). São Paolo: Fontes do Ipiranga, on wood, 16–24.I.1987 *Hjortstam 16515* (O, H).

Remarks. *Basidiodendron luteogriseum* is the generic type of *Basidiodendron*. For a long time, it was considered a synonym of *B. eyrei*. However, our study of the type material and newly collected specimens from Brazil revealed this viewpoint cannot be maintained. In addition to a clear genetic distance, *B. luteogriseum* can be distinguished from *B. eyrei* due to conspicuous, fishbone-like basidia-bearing hyphae emerging directly from subicular ones, as well as more regularly shaped, predominantly globose basidiospores with higher Q values.

Basidiodendron microsporum Spirin, V. Malysheva & Kotiranta, sp. nov. – Fig. 3

MB 834773

Holotype. Russia. Primorie: Spassk Dist., Spassk-Dalnii, *Populus* sp. (decorticated branch), 23.VII.2018 *Kotiranta 28653** (H, isotype – LE).

Etymology: microsporus (Lat., adj.) – having small spores.

Basidiocarps effused, covering a few mm, rarely up to 1 cm in widest dimension, first pruinose-reticulate, greyish, then continuous, brownish, gelatinized, smooth, 0.02–0.03 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, tightly arranged, hardly discernible, thin- to slightly thick-walled, subicular hyphae subparallel, 1–2 µm in diam., subhymenial hyphae interwoven or ascending, 1.5–2.5 µm in diam. Gloeocystidia abundant, clavate or tapering, (13–) 14–23 (–24) × (3.2–) 3.8–5.3 (–5.4) µm (n = 20/1); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, often sinuous, up to 11 × 2 µm; basidia four-celled, (6.1–) 6.2–7.3 (–7.8) × (4.6–) 4.9–6.2 (–6.4) µm (n = 20/1), senescent basidia slightly thick-walled, sterigmata up to 5 × 1–1.5 µm. Basidiospores thin-walled or with indistinctly thickened wall, ellipsoid to subglobose or globose, (3.2–) 3.3–4.1 (–4.2) × (2.8–) 2.9–3.8 (–3.9) µm (n = 30/1), L = 3.79, W = 3.26, Q' = (1.0–) 1.1–1.2 (–1.3), Q = 1.17, apiculus distinct to small, regular.

Remarks. *Basidiodendron microsporum* has the smallest basidia and basidiospores among the species treated here. Due to this feature, it can be differentiated from other species distributed in temperate – boreal forests of East Asia (*B. alni*, *B. eyrei*, *B. grandinioides*, *B. olivaceum*, *B. remotum* and *B. salebrosum*). *Basidiodendron microsporum* is so far known only from the type locality in Russian Far East.

Basidiodendron olivaceum Spirin & V. Malysheva, sp. nov. – Fig. 3

MB 834774

Holotype. Russia. Khabarovsk Reg.: Solnechnyi Dist., Razlivnaya, *Pinus pumila*, 23.VIII.2011 *Spirin 4304** (H, isotype – LE).

Etymology: olivaceus (Lat., adj.) – olivaceous.

Basidiocarps effused, covering a few mm, rarely up to 1 cm in widest dimension, first pruinose-reticulate, smooth, arid, ochraceous, then continuous, irregularly tuberculate, arid or only slightly gelatinized, dirty ochraceous to pale olivaceous-brown, 0.02–0.05 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, tightly arranged, thin- to slightly thick-walled, subicular hyphae interwoven, 2–3 µm in diam., subhymenial hyphae interwoven or ascending, 1.5–2.5 (–3) µm in diam. Gloeocystidia abundant, clavate or indistinctly tapering, (12–) 13–22 (–24) × (4.0–) 4.7–7.3 (–7.4) µm (n = 30/3), contents dark brown; hyphidia rarely present, simple or bifurcate, 1–1.5 µm in diam. at the apex. Basidia-bearing hyphae slightly thick-walled, hardly discernible, up to 30 × 2–3 µm; basidia four-celled, (6.4–) 6.8–9.1 (–9.2) × (5.1–) 5.3–7.1 (–7.7) µm (n = 38/4), senescent basidia slightly thick-walled, sterigmata up to 7 × 1.5–2 µm. Basidiospores thin-walled or with indistinctly thickened wall, ellipsoid to subglobose or globose, (3.3–) 3.4–5.1 (–5.2) × (2.8–) 2.9–4.7 µm (n = 120/4), L = 3.99–4.51, W = 3.29–4.06, Q' = (1.0–) 1.1–1.4 (–1.5), Q = 1.11–1.22, apiculus distinct to small, regular or eccentric.

Specimens examined. Canada. Alberta: Yellowhead Co., Whitehorse Wildland Provincial Park, *Picea glauca*, 26.VII.2015 *Spirin 8969** (ALTA, H). Russia. Khabarovsk Reg.: Solnechnyi Dist., Igdomi, *Pinus pumila*, 2.IX.2016 *Spirin 10780** (H), *Larix gmelinii*, 6.IX.2016 *Spirin 11014** (H), Razlivnaya (holotype, see above).

Remarks. *Basidiodendron olivaceum* is a sibling species of *B. deminutum* distributed in mountain coniferous forests of East Asia and North America. It differs from the European *B. deminutum* in having darker basidiocarps and shorter gloeocystidia with intensively coloured (resinous-brown) and strongly cyanophilous contents. Basidiospores of *B. olivaceum* are on average shorter and broader than in *B. deminutum* but these differences are merely statistical. So

far, *B. olivaceum* was detected on fallen but tough logs and branches of conifers (*Larix*, *Picea*, *Pinus*).

Basidiodendron parile Spirin & V. Malysheva, sp. nov. – Fig. 3

MB 834775

Holotype. Norway. Møre og Romsdal: Nesset, Eikesdalen, *Ulmus glabra*, 27.IX.2017 *Spirin 11607** (O, isotypes – H, LE).

Etymology: parilis (Lat., adj.) – equal, in reference to a regular basidiospore shape.

Basidiocarps effused, covering a few mm, pruinose-reticulate, smooth, waxy, greyish, 0.02–0.04 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, subicular hyphae thin- or slightly thick-walled and subparallel, 1–2 µm in diam., subhymenial hyphae thin- or slightly thick-walled, ascending or interwoven, 1–2 (–2.5) µm in diam. Gloeocystidia abundant, tapering, solitary or in groups of 2–3, (12–) 14–39 (–42) × (4.8–) 4.9–7.3 (–7.8) µm (n = 27/2); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 25 × 1.5–2 µm; basidia four-celled, (7.4–) 7.8–9.7 (–10.2) × (6.0–) 6.2–8.7 (–9.3) µm (n = 25/2), senescent basidia slightly thick-walled, sterigmata up to 5 × 1.2–2 µm. Basidiospores thin-walled or with indistinctly thickened wall, subglobose to globose, very rarely broadly ellipsoid, (4.2–) 4.7–5.9 (–6.1) × (4.0–) 4.1–5.6 (–5.9) µm (n = 60/2), L = 5.19–5.27, W = 4.97–5.02, Q' = 1.0–1.1 (–1.3), Q = 1.03–1.06, apiculus distinct to rather small, regular or eccentric.

Specimens examined. Norway. Vestfold: Larvik, Kvelde, Jordstøyp, *U. glabra*, 15.IX.2016 *Spirin 11099** (O). Møre og Romsdal (holotype, see above).

Remarks. *Basidiodendron parile* is introduced here based on two collections from Norway, both from very rotten wood of *Ulmus glabra*. Morphologically, it is most close to *B. globisporum* which, however, occurs on coniferous hosts. In addition to substrates, these species can be separated due to different shape and size of basidiospores (Fig. 4). Moreover, basidia of *B. parile* are considerably smaller than in *B. globisporum*.

Basidiodendron pelinum Alvarenga & K.H. Larss., sp. nov. – Fig. 3

MB 834776

Holotype. Brazil. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Barragem des Moças, angiosperm wood, 20.IV.2013 *Larsson 16014** (O, isotype – H).

Etymology: pelinos (Gr., adj.) – clay-coloured.

Basidiocarps effused, covering a few cm, first pruinose, then continuous, smooth or irregularly tuberculate, arid, pale ochraceous to greyish, 0.05–0.1 mm thick, in oldest parts unevenly cracking, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, subicular hyphae slightly thick-walled, subparallel, 3–3.5 µm in diam., subhymenial hyphae thin- or slightly thick-walled, interwoven, 2–3 (–3.5) µm in diam. Gloeocystidia abundant, broadly clavate or tapering, (15–) 17–30 (–35) × (5.6–) 5.7–9.6 (–10.0) µm (n = 30/2); hyphidia not seen. Basidia-bearing hyphae thin-walled, often strongly reduced and thus hardly discernible, occasionally distinct, up to 10 × 2–3.5 µm; basidia four-celled, (9.2–) 9.4–13.8 (–14.2) × (6.2–) 6.5–8.4 (–8.7) µm (n = 30/2), senescent basidia slightly thick-walled, sterigmata up to 8 × 2–3 µm. Basidiospores thin-walled, broadly ellipsoid to ellipsoid-ovoid, (4.6–) 4.9–7.1 (–7.8) × (3.8–) 3.9–5.2 (–5.3) µm (n = 60/2), L = 5.61–6.06, W = 4.32–4.56, Q' = (1.1–) 1.2–1.4 (–1.5), Q = 1.30–1.33, apiculus distinct, regular or more rarely eccentric.

Specimens examined. Brazil. Pernambuco: Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Barragem des Moças, angiosperm wood, 20.IV.2013 *Larsson 15985* (O, H), *Larsson 16014** (holotype, see above).

Remarks. *Basidiodendron pelinum* is introduced here based on two collections from Pernambuco, Brazil. In contrast to two other species treated here, *B. iniquum* and *B. luteogriseum*, *B. pelinum* does not produce so pronounced fishbone-like basidia-bearing hyphae, i.e. it is anatomically more similar to temperate – boreal species of the *B. eyrei* complex.

Basidiospores of *B. pelinum* are regularly shaped, ellipsoid, as a rule with a conventionally placed apiculus.

Basidiodendron remotum Spirin, V. Malysheva & Kotiranta, sp. nov. – Fig. 3

MB 834777

Holotype. Russia. Yakutia: Namsky Dist., Sielyakh, *Picea* sp., 18.VIII.1999 *Kotiranta 16308** (H 7039169, isotype – LE).

Etymology: remotus (Lat., adj.) – remote.

Basidiocarps effused, covering a few cm, first pruinose-reticulate, then continuous, smooth, waxy, greyish, 0.02–0.04 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, subicular hyphae slightly or distinctly thick-walled, subparallel, 1.5–2.5 µm in diam., subhymenial hyphae thin- or slightly thick-walled, interwoven or ascending, 1–2 µm in diam. Gloeocystidia abundant, tapering or clavate, some sinuous, occasionally pleural, (18–) 19–30 (–31) × (5.3–) 5.4–8.2 (–10.0) µm (n = 20/1); hyphidia not seen. Basidia-bearing hyphae slightly thick-walled, up to 25 × 2–2.5 µm; basidia four-celled, (6.3–) 7.2–8.9 (–9.1) × (5.2–) 5.3–6.6 (–6.8) µm (n = 20/1), sterigmata up to 4 × 1–1.5 µm. Basidiospores with slightly thickened wall (ca. 0.2 µm), compressed-ellipsoid to subglobose or rarely globose, (2.9–) 3.0–3.9 (–4.1) × (3.6–) 3.7–4.4 (–4.6) µm (n = 30/1), L = 3.43, W = 4.10, Q' = 0.7–0.9 (–1.0), Q = 0.84, apiculus distinct to small, often asymmetric, regular or eccentric.

Remarks. Predominantly compressed basidiospores of *B. remotum* are reminiscent of those of *B. eyrei* although they are clearly larger in the latter species. So far, *B. remotum* is known from a single locality in Siberia where it was collected on rotten wood of spruce.

Basidiodendron salebrosum Spirin & V. Malysheva, sp. nov. – Fig. 3

MB 834778

Holotype. Russia. Khabarovsk Reg.: Khabarovsk Dist., Malyi Niran, *Picea ajanensis*, 7.VIII.2012 *Spirin 5024** (H 7022939, isotype – LE).

Etymology: salebrosus (Lat., adj.) – uneven, rough.

Basidiocarps effused, covering a few cm, first pruinose-reticulate, then continuous, smooth, waxy or arid, greyish to pale ochraceous, 0.02–0.04 mm thick, margin gradually thinning-out. Hyphal structure monomitic, hyphae clamped, tightly arranged, thin-walled, subicular hyphae subparallel, 1.5–2 µm in diam., subhymenial hyphae interwoven or ascending, 2–2.5 µm in diam. Gloeocystidia abundant, distinctly tapering (bottle-shaped), (13–) 15–27.5 (–34) × (4.0–) 4.8–8.8 (–9.0) µm (n = 22/2); hyphidia not seen. Basidia-bearing hyphae thin-walled, often strongly reduced and thus hardly discernible, but occasionally distinct, up to 15 × 3–4 µm; basidia four-celled, (9.3–) 10.3–14.2 (–15.1) × (6.9–) 7.1–9.8 (–10.2) µm (n = 30/2), sterigmata up to 8 × 1.5–2 µm. Basidiospores thin-walled or with indistinctly thickened wall, ellipsoid to subglobose, (5.6–) 5.7–7.6 (–8.2) × (4.4–) 4.8–6.1 (–6.4) µm (n = 50/2), L = 6.49–6.68, W = 5.44–5.48, Q' = 1.1–1.4 (–1.5), Q = 1.19–1.23, apiculus distinct to small, often asymmetric, regular or eccentric.

Specimens examined. Russia. Khabarovsk Reg.: Khabarovsk Dist. (holotype, see above); Solnechnyi Dist., Igdomi, *P. ajanensis*, 3.IX.2016 Spirin *10900** (H).

Remarks. Large, ellipsoid or subglobose basidiospores with an asymmetric apiculus differentiate *B. salebrosum* from other species dealt with above, as well as from *B. caesiocinereum* s.l. The species was found twice in Russian Far East, and both records were from decorticated but rather tough spruce logs.

Key for globose- or ellipsoid-spored *Basidiodendron* species in temperate – boreal Eurasia (only species with basidiospores under 8 µm in largest dimension are treated)

1. Basidiospores 5.5–7.5 µm in largest dimension ……..……..…… 2

(1). Basidiospores smaller ……..…….. 3

2. Basidiospores ellipsoid to subglobose, smooth. East Asian species ……. *B. salebrosum*

(2). Basidiospores globose or compressed-subglobose, sometimes warted … *B. caesiocinereum* s.l.

3. Basidiospores compressed-subglobose to globose …… 4

(3). At least some basidiospores ellipsoid or broadly ellipsoid ……. 6

4. On conifers. Apiculus regular …….. *B. globisporum*

(4). On angiosperms. Apiculus of some spores eccentric, asymmetric ……. 5

5. Basidia up to 11.5 µm long, gloeocystidia up to 65 µm long, basidiospores more or less regularly subglobose or globose. East Asian species …….. *B. alni*

(5). Basidia up to 13.5 µm long, gloeocystidia up to 45 µm long, at least some basidiospores clearly compressed ……..…….. *B. eyrei*

6. Basidia up to 13.5 µm long, apiculus mostly eccentric ……..…….. *B. eyrei*

(6). Basidia up to 9.5 µm long, apiculus regular or eccentric ……. 7

7. On conifers ……... 8

(7). On angiosperms ……..…… 11

8. Europe and Caucasus …….. 9

(8). East Asia and North America …….. 10

9. Hymenophore grandinioid, basidiospores predominantly subglobose or globose ……. *B. caucasicum*

(9). Hymenophore smooth, basidiospores predominantly cylindrical or ellipsoid ……. *B. deminutum*

10. Basidiospores compressed-ellipsoid or subglobose to globose, 3–4 × 3.5–4.5 µm ……. *B. remotum*

(10). Basidiospores ellipsoid to subglobose, 3.5–5 × 3–4.5 µm …….. *B. olivaceum*

11. Hymenophore grandinioid …….. 12

(11). Hymenophore smooth …….. 13

12. Basidiospores compressed-subglobose, 3–3.7 × 3.2–4 µm. North America …….. *B. fulvum*

(12). Basidiospores mostly ellipsoid, 4–6 × 3–5 µm. Eurasia ……. *B. grandinioides*

13. Basidiospores 4.5–6 × 4–5.5 µm. Europe ……..…… *B. parile*

(13). Basidiospores 3.5–4 × 3–4 µm. East Asia ……..…. *B. microsporum*

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Figures

Fig. 1. Combined nrITS+nrLSU topology from maximum likelihood analysis showing main lineages within *Auriculariales*. All sequences generated for this study are indicated in bold. GenBank/UNITE or collection numbers (for newly generated sequences) are given for all sequences. Support values (ML/BA) are given above the branches. Scale bar shows expected changes per site.

Fig. 2. Combined nrITS+*tef1* topology from maximum likelihood analysis showing phylogenetic relationships of *Basidiodendron* species. All sequences generated for this study are indicated in bold. GenBank/UNITE or collection numbers (for newly generated sequences) are given for all sequences. Support values (ML/BA) are given on the branches. Scale bar shows expected changes per site.

Fig. 3. Basidiospores of *B. eyrei* and related species: a – *B. alni* (holotype); b – *B. caucasicum* (holotype); c – *Basidiodendron deminutum* (lectotype); d – *Bourdotia rimulenta* (lectotype); e – *B. mucosa* (lectotype); f – *Basidiodendron eyrei* (Kotiranta 26231); g – *B. globisporum* (Spirin 7040); h – *B. grandinioides* (lectotype); i – *B. iniquum* (holotype); j – *B. luteogriseum* (five left – lectotype, two right – Larsson 16022); k – *B. microsporum* (holotype); l – *B. olivaceum* (Spirin 11014); m – *B. parile* (holotype); n – *B. pelinum* (holotype); o – *B. remotum* (holotype); p – *B. salebrosum* (holotype). Scale bar = 5 µm. As depicted, the basidiospore's longitudinal axis corresponds to its length and transversal axis to its width (see further explanations in Material and methods).

Fig. 4. Basidiocarps of *B. eyrei* (Spirin 13060).

Fig. 5. Microscopic structures of *B. globisporum* (Spirin 7040): a – gloeocystidia with hyphoid apical outgrowths; b – normally developed gloeocystidia; c – basidia-bearing hypha covered by collapsed basidial cells; d – turgid basidia; e – basidiospores. Scale bar = 10 µm.

Fig. 6. Microscopic structures of *B. luteogriseum* (Larsson 16022): a – basidia-bearing hypha with collapsed basidial cells, turgid basidia and gloeocystidia; b – basidiospores. Scale bar = 10 µm.

Table 1

DNA sequences generated for the present study

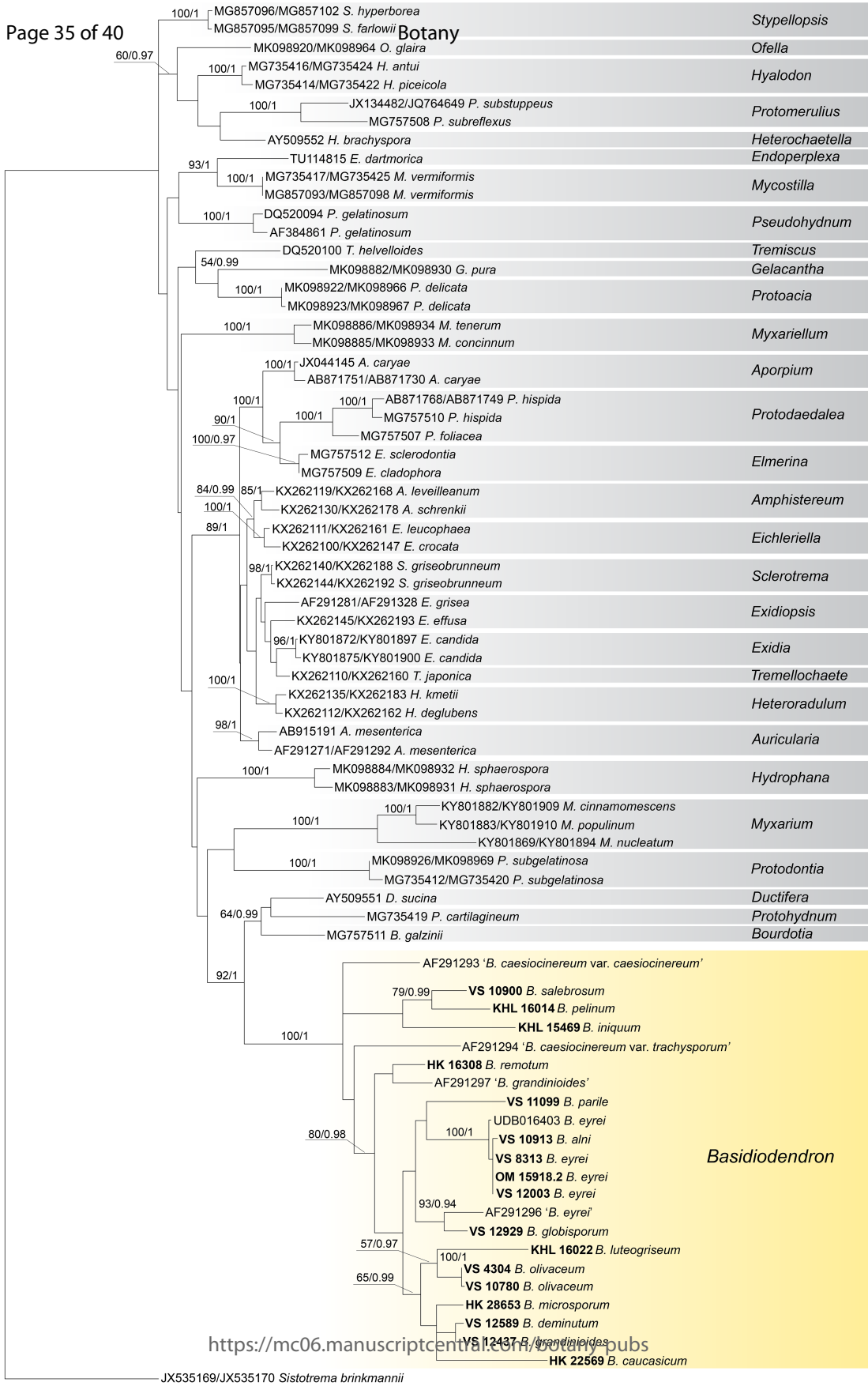
Species	Specimen / herbarium	Country (ISO code)	Host	GenBank sequence numbers		
				nrITS	nrLSU	*tef1*
Basidiodendron alni	HK26050 (H)	RU-KRA	*Alnus hirsuta*	MT040878	-	MT055847
B. alni	VS 10913 (H)	RU-KHA	*A. hirsuta*	MT040869	-	-
B. caucasicum	HK 22569 (H)	RU-AD	*Pinus sylvestris*	MT040877	MT040856	MT055855
B. deminutum	VS 12589 (H)	SI	*Pinus mugo*	MT040885	MT040865	MT074092
B. eyrei	VS 8881 (H)	CA-BC	*Picea* sp.	MT040868	-	-
B. eyrei	VS 12363 (TU)	EE	*Alnus incana*	UDB0754285	-	-
B. eyrei	HK 26231 (H)	RU-KRA	*Betula* sp.	MT040874	-	MT055845
B. eyrei	VS 10579 (H)	RU-NIZ	*Tilia cordata*	MT040866	-	MT055844
B. eyrei	VS 12003 (H)	RU-NIZ	*T. cordata*	MT040880	MT040854	MT055846
B. eyrei	OM 15918.2 (H)	ES	*Abies pinsapo*	MT035841	MT035841	-
B. eyrei	OM 13649	CH	*Fagus sylvatica* (?)	MT040879	MT062853	
B. eyrei	VS 8313 (H)	US-WA	*Arbutus menziesii*	MT040882	MT040855	MT071080
B. globisporum	VS 7040 (H)	RU-LEN	*Picea abies*	MT040872	-	MT055852
B. globisporum	VS 12929 (H)	RU-LEN	*P. abies*	MT040884	MT040864	-
B. globisporum	VS 13450 (H)	SI	*P. abies*	MT040888	-	MT055859
B. globisporum	OM 15584 (H)	US-NY	*Tsuga* sp.	MT040886	-	-
B. grandinioides	VS 12437 (O)	NO	*Ulmus glabra*	MT040873	MT040863	MT055854
B. grandinioides	AS 11315 (S)	NO	angiosperm	MT040887	-	-
B. iniquum	KHL 15469 (O)	BR	angiosperm	MT040876	-	-
B. luteogriseum	KHL 16022 (O)	BR	angiosperm	MT040881	MT040861	MT055857
B. microsporum	HK 28653 (H)	RU-PRI	*Populus* sp.	-	MT040859	MT055856
B. olivaceum	VS 8969 (ALTA)	CA-AB	*Picea glauca*	MT040870	-	MT055848
B. olivaceum	VS 4304 (H)	RU-KHA	*Pinus pumila*	MT040883	MT040857	MT055851
B. olivaceum	VS 10780 (H)	RU-KHA	*P. pumila*	-	MT040858	MT055849
B. olivaceum	VS 11014 (H)	RU-KHA	*Larix gmelinii*	MT040867	-	MT055850
B. parile	VS 11099 (O)	NO	*U. glabra*	MT040890	-	-

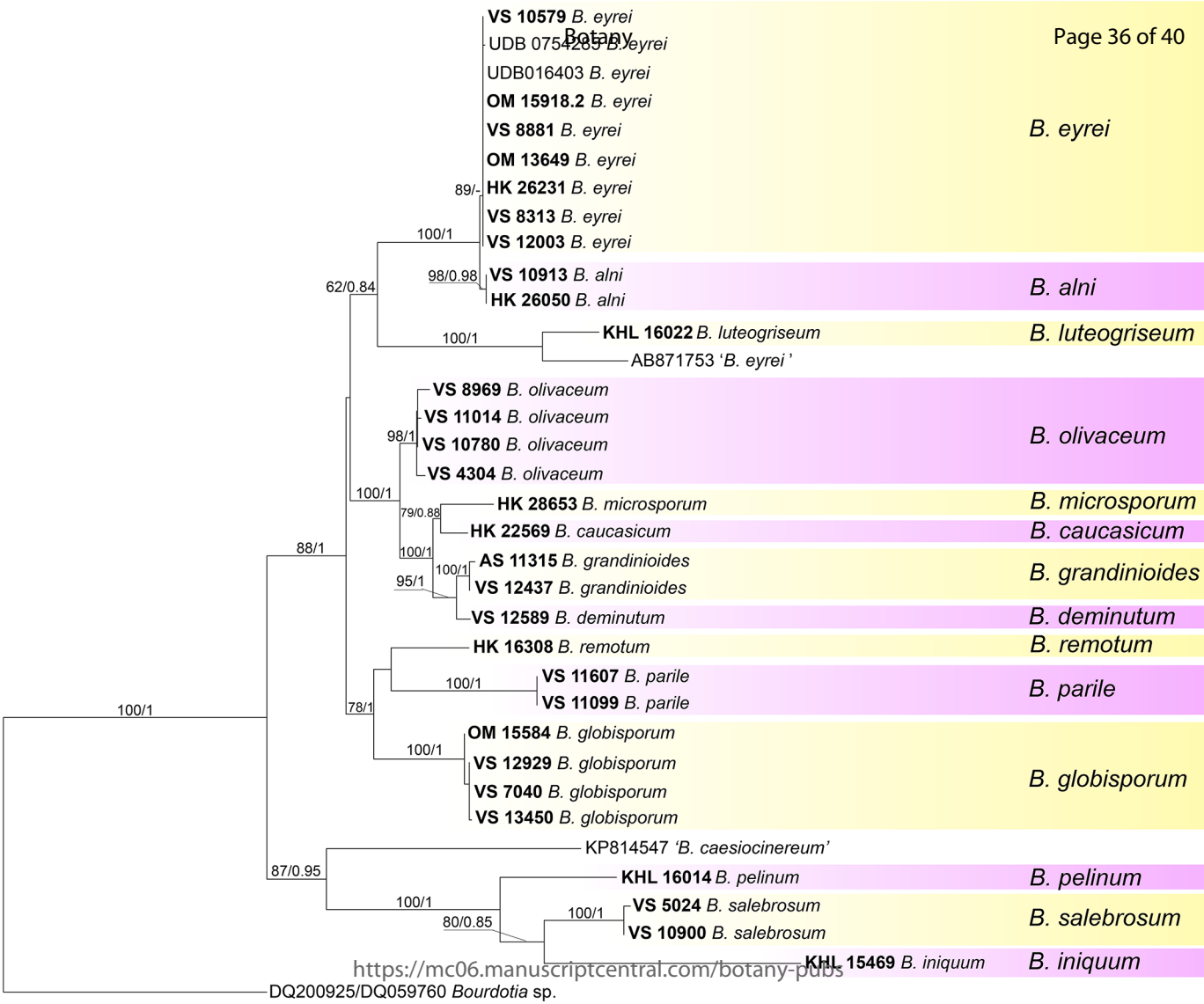
B. parile	VS 11607 (O)	NO	*U. glabra*	MT040889	-	MT055860
B. pelinum	KHL 16014 (O)	BR	angiosperm	MT040875	MT040862	MT055858
B. remotum	HK 16308 (H)	RU-SA	*Picea* sp.	-	MT040860	MT055853
B. salebrosum	VS 5024 (H)	RU-KHA	*Picea ajanensis*	MT040871	-	-
B. salebrosum	VS 10900 (H)	RU-KHA	*P. ajanensis*	MT040891	-	-

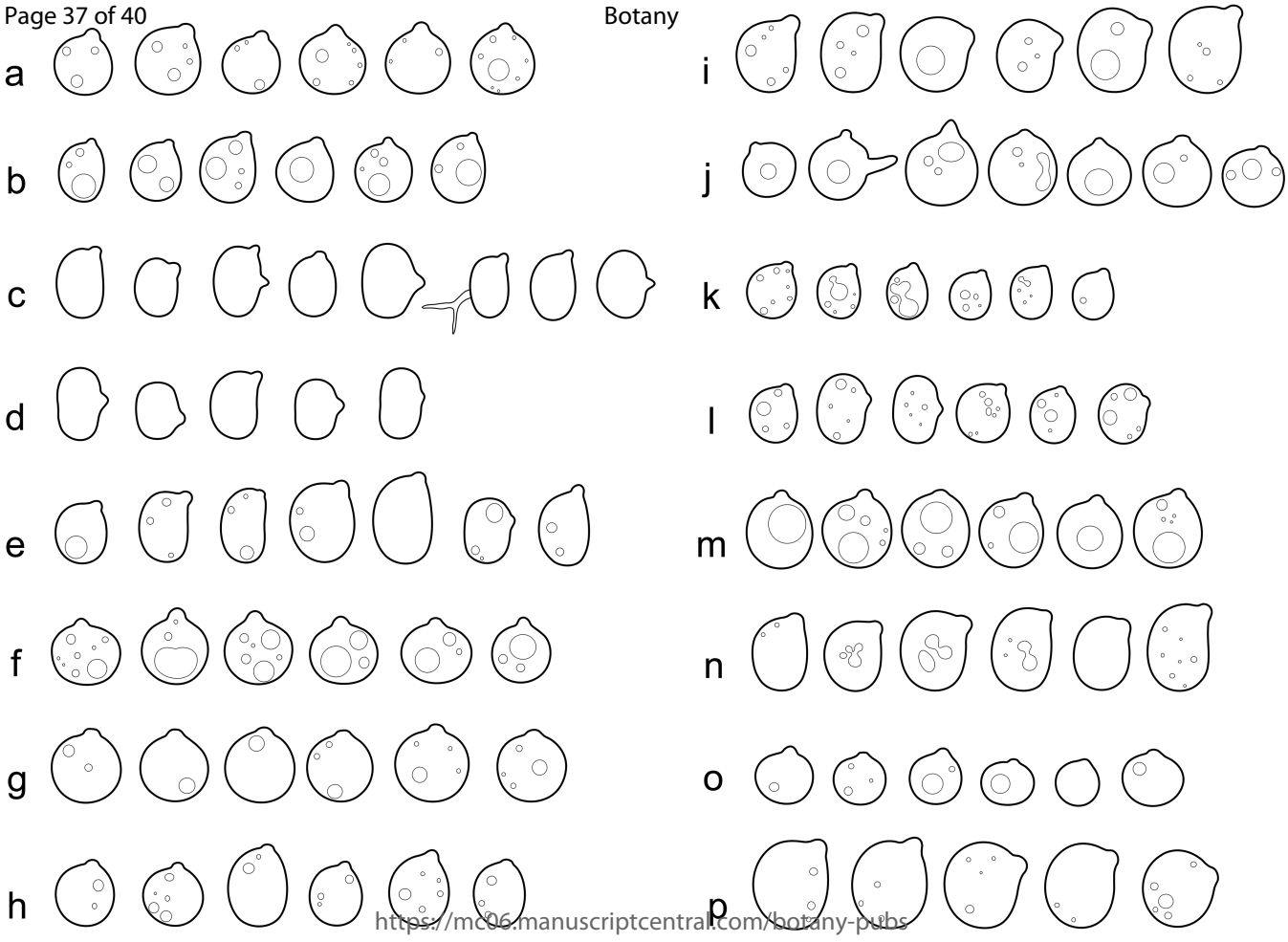
Table 2

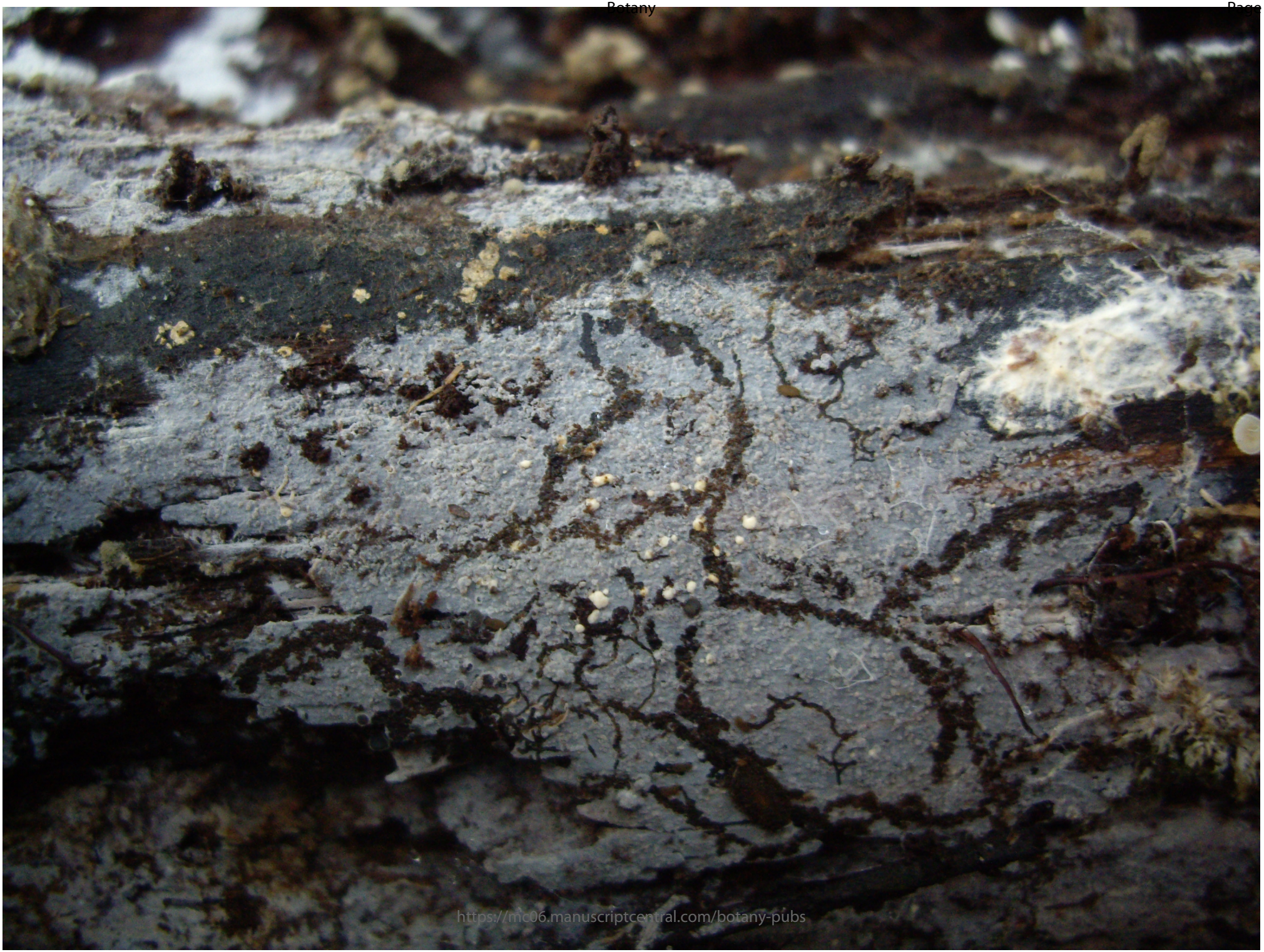
Geographic, ecological and morphological traits in *Basidiodendron eyrei* complex

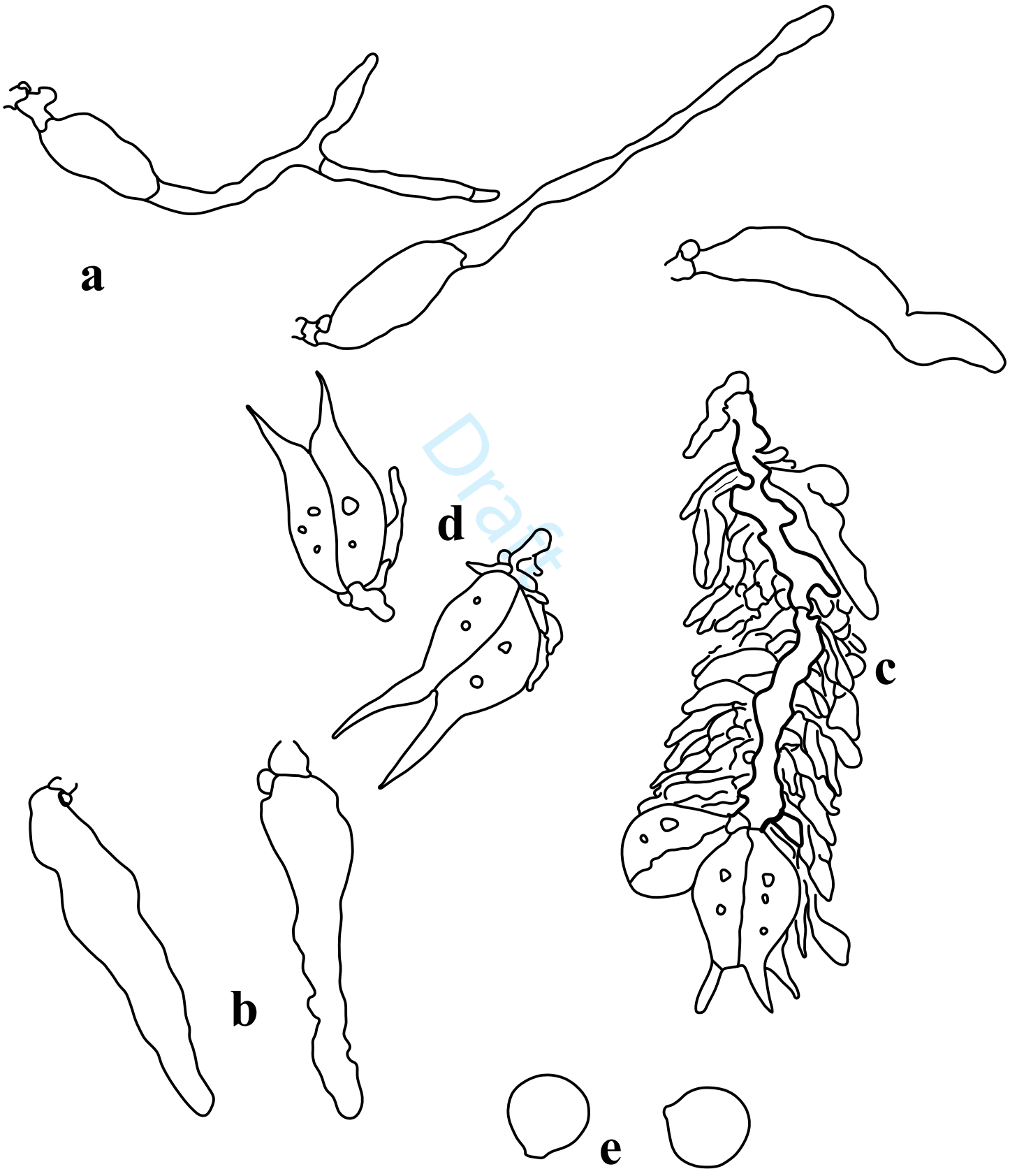
Species	Geographic distribution	Host	Basidiocarps	Basidial size, µm	Basidiospores
B. alni	East Asia, boreal	angiosperms (*Alnus*)	smooth, pale coloured	9–11.5 × 6–8	predominantly globose, 4.1–5.0 × 4.2–5.0 µm, Q = 0.99
B. caucasicum	Europe (Caucasus), warm temperate	gymnosperms (*Pinus*)	smooth or grandinioid, pale coloured	7.5–9.5 × 6–7	subglobose or globose, 4.0–5.1 × 3.4–4.5 µm, Q = 1.15
B. deminutum	Europe, warm temperate	gymnosperms (*Pinus*)	smooth, pale coloured to brownish	7.5–9.5 × 5.5–7	cylindrical to broadly ellipsoid or subglobose, 4.1–5.6 × 2.9–4.7 µm, Q = 1.23–1.51
B. eyrei	Eurasia and North America, temperate – hemiboreal	almost exclusively angiosperms	smooth, pale coloured to brownish	8.5–13 × 6–8	compressed-subglobose to almost globose, 3.8–5.2 × 4.2–5.4 µm, Q = 0.88–0.97
B. globisporum	Europe and North America, temperate – boreal	gymnosperms (*Picea, Tsuga*)	smooth, pale coloured	9–12 × 7–9	compressed-subglobose to globose, 4.6–5.8 × 4.8–5.9 µm, Q = 0.96–0.98
B. grandinioides	Europe, temperate – hemiboreal	angiosperms	smooth or grandinioid, pale coloured	8–11.5 × 6–8	ellipsoid to broadly ellipsoid, 4.0–6.0 × 3.1–4.9 µm, Q = 1.22–1.36
B. iniquum	South America, tropical	angiosperms	smooth, pale coloured	9.5–13 × 7.5–9	ellipsoid to broadly ellipsoid, 4.9–6.2 × 4.1–5.2 µm, Q = 1.19
B. luteogriseum	South America, tropical	angiosperms	smooth, pale coloured	8–10 × 6–8	compressed-subglobose to globose, 4.1–5.1 × 4.0–5.1 µm, Q = 0.94–1.03
B. microsporum	East Asia, temperate	angiosperms (*Populus*)	smooth, pale coloured to brownish	6–7.5 × 5–6	ellipsoid to subglobose, 3.3–4.1 × 2.9–3.8 µm, Q = 1.17
B. olivaceum	East Asia and North America, boreal	gymnosperms	smooth, ochraceous to olivaceous-brown	7–9 × 5.5–7	ellipsoid to subglobose, 3.4–5.1 × 2.9–4.7 µm, Q = 1.11–1.22
B. parile	Europe, temperate – hemiboreal	angiosperms (*Ulmus*)	smooth, pale coloured	8–9.5 × 6–8.5	subglobose to globose, 4.7–5.9 × 4.1–5.6 µm, Q = 1.03–1.06
B. pelinum	South America, tropical	angiosperms	smooth, pale ochraceous	9.5–14 × 6.5–8.5	broadly ellipsoid to ellipsoid-ovoid, 4.9–7.1 × 3.9–5.2 µm, Q = 1.30–1.33
B. remotum	East Asia, boreal	gymnosperms (*Picea*)	smooth, pale coloured	7–9 × 5.5–6.5	compressed-ellipsoid to subglobose, 3.0–3.9 × 3.7–4.4 µm, Q = 0.84
B. salebrosum	East Asia, temperate – boreal	gymnosperms (*Picea*)	smooth, pale coloured	10.5–14 × 7–10	ellipsoid to subglobose, 5.7–7.6 × 4.8–6.1 µm, Q = 1.19–1.23

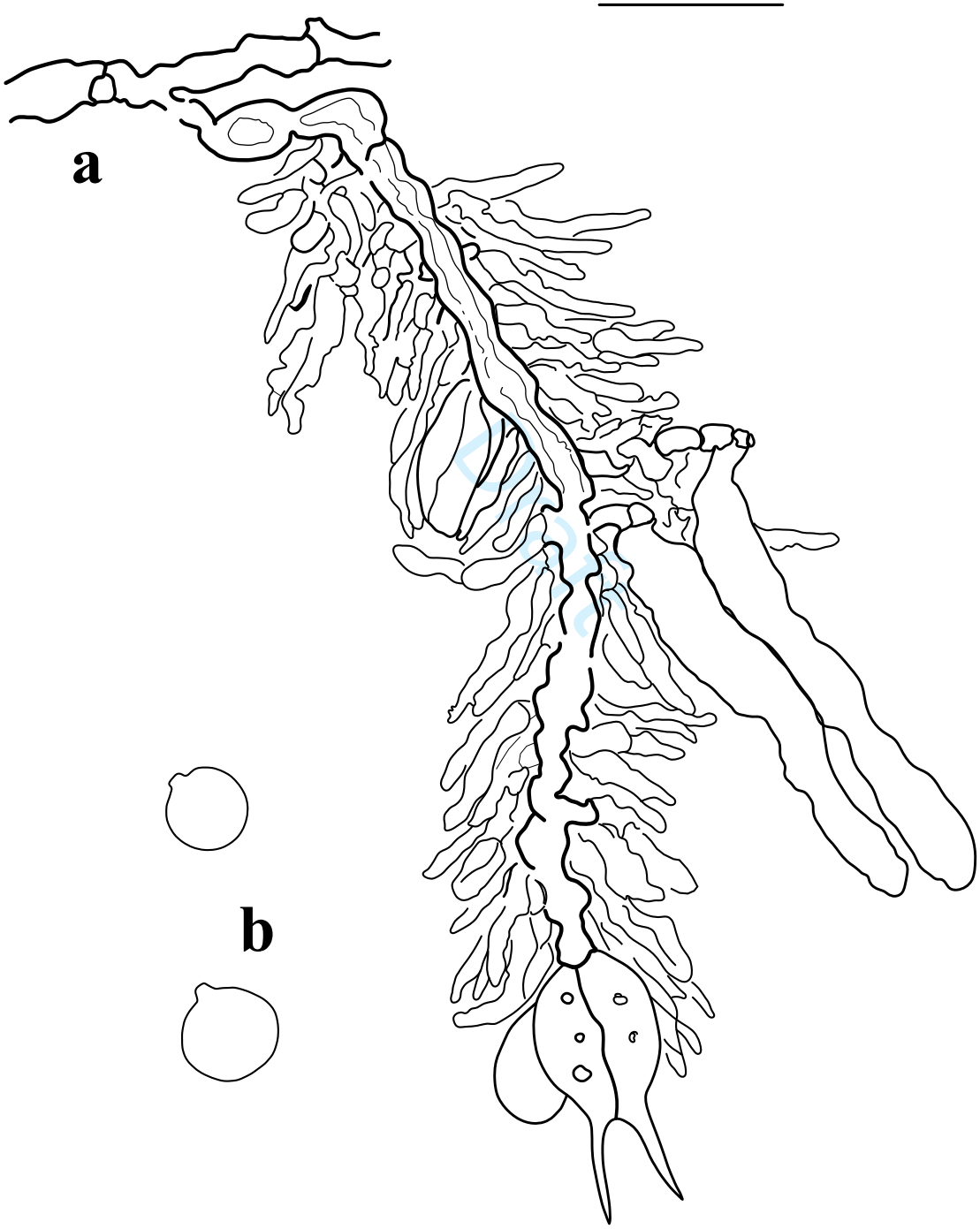











a
b